Studies in New Zealand *Cotulas*

By Elizabeth Edgar

University of Canterbury

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Part I.—Floret Types and Natural Groupings of the Species.

Abstract

Previous descriptions of the disc florets of the endemic New Zealand *Cotulas,* which belong to the section Leptinella, have proved to be confusing, since it has never been emphasised that these florets are male, in contrast to the hermaphrodite disc florets of the sections Eucotula and Strongylosperma.

The types of floret found in the three sections of *Cotula* are described, and variations in the proportions of the sexes in the capitulum are noted for some species. It is shown that the endemic New Zealand *Cotulas* can be divided into two groups on the basis of their stem anatomy and the correlations of this grouping with the distribution of the sexes, flower colour, and ecological characters are discussed.

The genus *Cotula,* comprising some fifty species, is widely dispersed throughout the world, more especially in the Southern Hemisphere. Bentham (1863) subdivides the genus into three sections—Eucotula, Strongylosperma and Leptinella, a classification based on the differences in the female florets and their arrangement on the heads. Before this time the genus *Cotula* consisted of Eucotula only, and the other sections of the genus as at present constituted were at one time ranked as separate genera. The characters of the capitulum in the three sections of the genus are as follows:—

Section I. Eucotula (Fig. 1a)

Receptacle flat or convex, achenes of the female florets on long stalks, in a single row. Female florets without any corolla. Disc florets hermaphrodite, on much shorter pedicels, very numerous; corolla tubular.

Section II. Strongylosperma (Fig. 1b)

Receptacle flat or convex, achenes of the female florets numerous, in several rows, sessile or stipitate. Female florets without any corolla. Disc florets hermaphrodite, comparatively few, subsessile; corolla tubular.

Section III. Leptinella (Fig. 1c)

Receptacle conical. Achenes of the female florets in several rows, sessile or shortly stipitate. Female florets with a short corolla Disc florets sterile, style undivided; corolla funnel-shaped.

The New Zealand species of *Cotula* belong to the section Leptinella, with the exception of *Cotula coronopifolia* (Section Eucotula) and *C. australis* (Section Strongylosperma) both of which species are widespread elsewhere. *Leptinella* was founded as a genus by Cassini in 1822 and later taken up by W. J. Hooker (1841) when he described some plants from South America under that genus. In the "*Flora Tasmaniae*" J. D. Hooker draws attention to the following distinctions between *Leptinella* and *Cotula.* Leptinella is restricted in its distribution to a subantarctic range, species being confined to New Zealand, Tasmania, Australia, the Auckland and Campbell Islands, Kerguelen Island and Fuegia. The section Eucotula,

on the other hand, has its main centre in South Africa, and is widespread in many temperate and tropical regions. Again there are several differences in the female florets. Hooker says of *Leptinella*: "The most peculiar character consists in the frequently inflated flowers of the ray whose corolla is formed of two layers with an intervening hollow space." In complete contrast to this the ray florets in the section Eucotula have normally no corolla at all. Hooker also notes the conspicuous glands on the florets of *Leptinella.* These are also present in Eucotula but are not so large.

The principal difference, however, between Eucotula and Leptinella is that in Eucotula the disc florets are hermaphrodite, but in Leptinella the disc florets are functionally male. Cassini's original description of *Leptinella,* quoted by Hooker in the "*Flora Antarctica*" says "floribus disci abortu masculis" (the disc florets are male through abortion). In this flora Hooker notes, "In all the plants of the genus which I have examined the heads of flowers are monoecious." In the "*Flora Novae-Zelandiae*" Hooker describes the heads of *Leptinella* as follows: ''Creeping monoecious or dioecious herbs. Flowers of the disc hermaphrodite, tubular with a four-toothed corolla, and a style ending in a cup or disc. Achaenium abortive . . . . Capitulum homogamum v. heterogamum . . . . Herbae facie *Cotuleae* monoicae v. dioicae . . . . Fl. disci steriles. . . . Achaenium fl. nullum vel breve stipitiforme." (Capitulum homogamous or heterogamous . . . . monoecious or dioecious *Cotula*-like herbs . . . . Disc florets hermaphrodite, sterile. Achenes of the hermaphrodite florets none, or short and stalk-shaped.) Here Hooker, in speaking of sterile hermaphrodite florets, is in accord with Bentham (1873) who said—"with regard to the individual florets (of Compositae), it is usual to distinguish four kinds—hermaphrodite, male, female and neuter; but the sterility of the pistil is often so uncertain in the anther-bearing flowers, in which it is never absolutely deficient, that I have found it much more convenient to designate as hermaphrodite all flowers having perfect anthers, whether their pistil be susceptible of fertilization or not, distinguishing them as fertile or sterile."

However, in the "Handbook of the New Zealand Flora" (1867) Hooker, in his generic description of *Cotula,* which by this time included *Leptinella,* wrote, "Heads unisexual, or the outer florets female, the inner *male.*" Here Hooker in using the term *male* has departed from Bentham's convention of calling all anther bearing florets hermaphrodite. Hooker drew up his generic description of *Cotula* to include only the New Zealand Leptinellas and his description is not applicable to either *Cotula coronopifolia* or *C. australis* although he enumerates these two species in the body of the work.

Kirk (1899) gives a generic description which covers the three sections of the genus and not just the New Zealand Leptinellas. "Outer florets in 1 or more rows, female; corolla short, broad, conical or 0. Disc-florets numerous, hermaphrodite, 4-5 toothed, *sometimes sterile.* . . . Heads . . . rarely dioecious." In describing the monoecious species he usually adheres to Bentham's convention of calling all disc florets hermaphrodite, but in his notes to the species he describes the disc florets as male.

Cheeseman's (1925) generic description also covers all three sections of the genus. He writes of the heads, "Heterogamous or rarely homogamous* through the suppression of the female florets; sometimes dioecious. Female florets exterior, in 1 or 2 series, fertile. Disc florets hermaphrodite or often male." Cheeseman has also departed from Bentham's convention of calling all disc florets hermaphrodite, and has revived the term *male* for the sterile hermaphrodites as Hooker had done before him in the "Handbook". But by drawing attention to the small abortive achenes

* The homogamous heads mentioned by Cheeseman, and not referred to by either Hooker or Kirk, occur in some South African species belonging to the section Eucotula, which have heads that are entirely hermaphrodite. The term *homogamous* which is applied to the capitula of Compositae when the florets are all alike, is not used by Cheeseman for dioecious species. For these he uses the term unisexual.

of the disc florets in three species only (*Cotula plumosa, C. lanata* and *C. Maniototo*), he might well be thought to imply that these achenes in the other endemic New Zealand species were neither small nor abortive and consequently that they had truly hermaphrodite florets. It is interesting, too, that Hoffman, in the Pflanzenfamilien (1897) gives an incomplete description of Cotula, for he makes no mention of the dioecious New Zealand species, nor does he state that the central disc florets in some species are functionally male, and so Yampolsky, C. & H. (1922) who based their paper on the descriptions given in Engler's Pflanzenfamilien, group *Cotula* with genera that have hermaphrodite or gynomonoecious species. In *Cotula,* the hermaphrodite species are the South African ones in which the outer female florets have been lost by abortion, the gynomonoecious species are the Eucotula type with outer female florets and central hermaphrodite florets. So the peculiar character of the Leptinella section of *Cotula,* with its monoecious and dioecious species, is not taken into account in either of these European works.

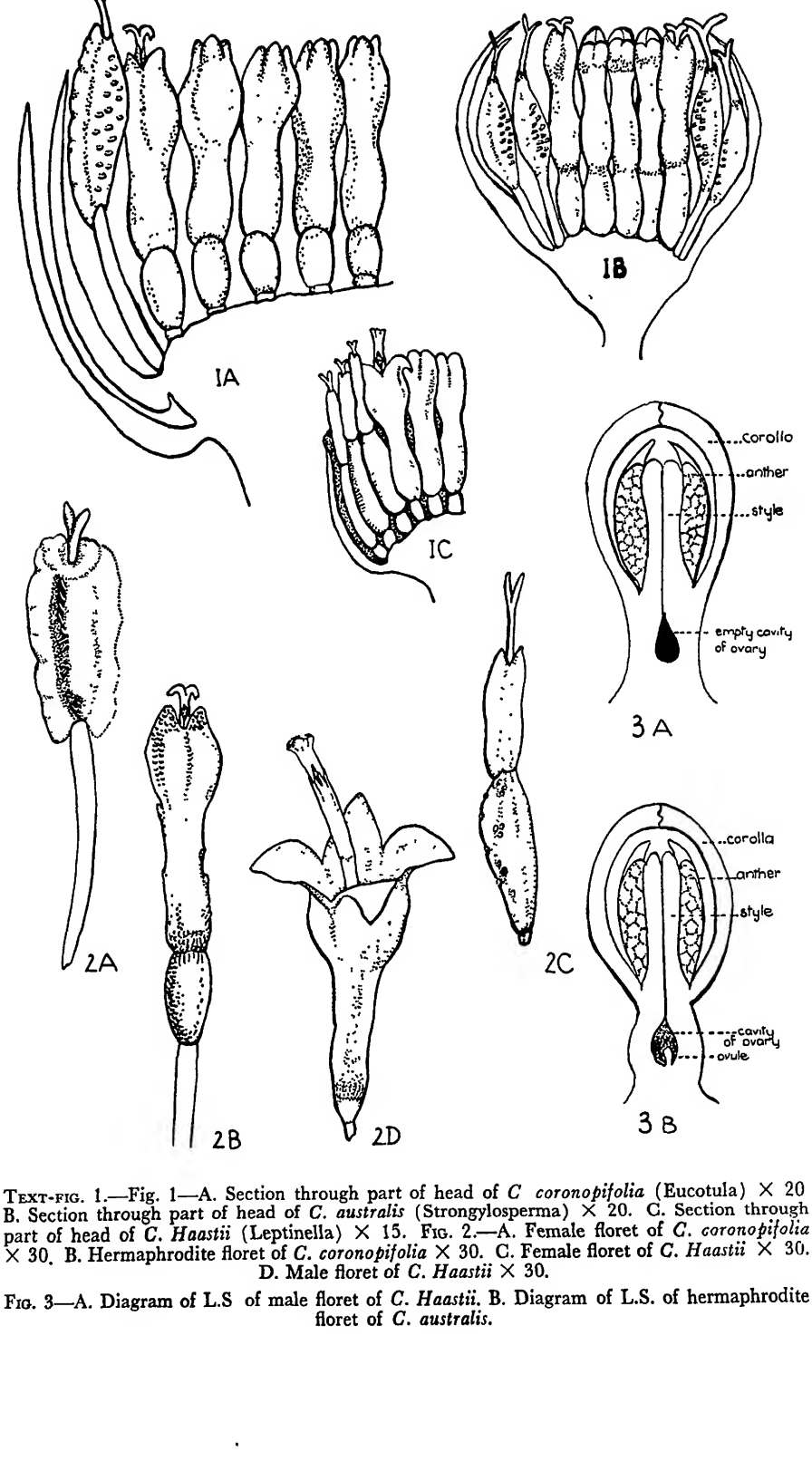
It was therefore difficult to determine from the New Zealand floras the true nature of the central florets in the endemic New Zealand *Cotulas,* because the authors of these floras used a terminology which was not uniform. Furthermore, the subdivision of the genus into sections was based on the characters of the female florets only, so that after *Leptinella* was included in *Cotula* the marked difference between the functionally male central florets of the Leptinella section and the truly hermaphrodite central florets of the Eucotula section was never emphasized, and, in fact, passed over by Hoffman and Yampolsky, C. & H. In view of this it was felt that the exact nature of the central florets would have to be ascertained for as many of the New Zealand species as possible. Isolated plants, therefore, of *Cotula Haastii, C. pectinata, C. atrata, C. minor, C. Maniototo, C. plumosa* and *C. lanata* were first found to set no seed on the disc florets. As this might have been due to self-incompatibility, as many of the species as possible were observed in the field in natural populations, and there again no seed was found set on the disc florets. This shows that these florets are functionally male.

TYPES OF FLORET IN *Cotula*

There are three main types of floret found in *Cotula*: female, hermaphrodite and male.

1. *The female florets*: (Fig. 2) are present in one or more outer rings in all species (other than the dioecious ones), with the exception of some South African species where they have been lost through abortion and the heads are composed entirely of hermaphrodite florets. (These are the homogamous heads mentioned by Cheeseman (1925), but there are no species of *Cotula* with this type of head in New Zealand.) There are two kinds of female floret, as has been noted in the preceding section. There is the type which occurs in the sections Eucotula and Strongylosperma, which is long-stalked, with its corolla so reduced as to be almost non-existent, and its gland-covered ovary with two broad spongy wings, the short bifid stigma being sunk in a notch between these wings. Two species in New Zealand, *Cotula coronopifolia* (Fig. 2A) and *C. australis* have this type of female floret. The contrast between this type of floret and the Leptinella female floret, which occurs in all the other New Zealand species, has already been mentioned, the principal difference being the presence of the corolla in Leptinella. In some species this corolla is a small tube inflated at the base, and narrowed into a minutely four-toothed mouth. This occurs, for example, in *Cotula haastii* (Fig. 2c), *C. pectinata, C. dioica* and *C. squalida.* In other species, *Cotula atrata* and *C. pyrethrifolia,* the corolla is not so compressed and is obviously lobed at the mouth.

The stigma in these female florets is the bifid stigma characteristic of female florets throughout the Compositae, though at times the style arms are extremely short, as is noted by Kirk for several of the species. Bentham (1873) writes of the styles



TEXT-FIG. 1.—Fig. 1—A. Section through part of head of *C coronopifolia* (Eucotula) × 20 B. Section through part of head of *C. australis* (Strongylosperma) × 20. C. Section through part of head of *C. Haastii* (Leptinella) × 15. FIG. 2.—A. Female floret of *C. coronopifolia* × 30. B. Hermaphrodite floret of *C. coronopifolia* × 30. C. Female floret of *C. Haastii* × 30. D. Male floret of *C. Haastii* × 30.

FIG. 3—A. Diagram of L.S of male floret of *C. Haastii*. B. Diagram of L.S. of hermaphrodite floret of *C. australis*.

of the female florets of the Compositae, " These styles of the female florets are uniformly divided into two equal, more or less stigmatic branches, glabrous without and papillose inside, which may occasionally vary in length or thickness, but only slightly so, and very rarely, as far as I have been able to observe, so as to give any but a very slight generic clue." For this reason the description given by Petrie (1885) of the stigma of the female floret of *Cotula Goyeni* seemed to point to a remarkable exception. This description is as follows: " Style crowned by a thin disc-like flattened stigma in *both female and hermaphrodite flowers.* . . . In some specimens the stigmatic disc shows traces of a division into two lobes but I have seen none with anything like two branches to the style. . . . If this peculiarity should prove constant in the present species, and it should continue to be regarded as a *Cotula,* the character of the genus as now formulated will require modification." Heads of the type specimen from Petrie's herbarium were examined, and it was concluded that although the style arms were very small and compressed for a female Composite stigma, the division into two lobes was always present and that this stigma was quite distinct from the club-shaped, flat-topped stigma of the male floret to which Petrie had compared it.

2. *The hermaphrodite florets*: of *Cotula coronopifolia* (Fig. 2B) and *C. australis* —belonging to the Eucotula and Strongylosperma sections respectively—have a tubular corolla, broadening to a four-lobed mouth and the ring of anthers surrounding the stigma are those typical of the tribe Anthemideae, having no tails. The stigma is bifid, of the type which Bentham termed the *Senecio* style, and he notes that it occurs in the Anthemideae. He describes this style as having flattened branches, narrow and recurved, with marginal stigmatic series which reach to the extremity, which is truncate and fringed with hairs.

3. *The male florets*: resemble the hermaphrodite florets of the other two sections in so far as they have a similar corolla and anthers. They differ, however, in the character of the stigma which is discoid and undivided, with hairs round the rim, but no stigmatic papillae (Fig. 2D). To quote Bentham once more: " In all tribes which admit of central sterile hermaphrodite florets (Asteroideae, Inuloideae, Helianthoideae, Helenoideae, Anthemideae, Senecionideae, Calendulaceae and Arctotideae) the styles of these sterile florets are for the most part filiform or slightly clavate, undivided or with slender erect branches, very papillose or hirsute outside, without stigmatic series inside, and very similar in all the different tribes where they occur." The stigma of the male floret, then, has retained what Bentham has termed its " principal and often sole function of sweeping the pollen out of the antheral tube " but (without a stigmatic surface) it has lost the function of allowing the pollen grains to germinate.

(a) *The abortion of the ovule in the male floret.*

Although the disc shaped stigma in the male floret was found to have no stigmatic papillae and had therefore lost the function of allowing the pollen to germinate, it was possible that the ovary beneath this sterile pistil might still be functional, despite the fact that it invariably appeared to be minute. The development, therefore of the ovary of *Cotula Haastii,* in which the disc florets set no seed, was investigated and compared with that of the hermaphrodite disc florets of *Cotula australis* on which seed is set.

(i) *Materials and method.*

Whole heads of *Cotula Haastii* and *C. australis* were killed and fixed in formalin-aceto-alcohol. Dehydration was carried out by passing through a graded series of tertiary butyl alcohol solutions (Johansen, 1940). The heads were embedded in paraffin wax and microtome sections were cut longitudinally through them. Sections were stained with Heidenhain's iron haematoxylin.

(ii) *Comparison of the Ovary in* Cotula Haastii *and* C. australis.

The development of the ovary is the same in the two species up to the formation of the cavity into which the ovule normally forms. In *Cotula Haastii,* however, no ovule develops, whereas in *Cotula australis* an ovule develops normally. If sections of *Cotula Haastii* and *C. australis* at similar ages are compared, an empty cavity can be seen in the ovary of *C. Haastii* below the base of the style (Fig. 3A), whereas in *C. australis* the ovule can be seen protruding into this cavity (Fig. 3B). Male florets of *Cotula Haastii* at a later stage than this show that the ovary has enlarged very little more, and that the cavity of the ovary is almost obliterated.

(b) *The development of the stigma of the male floret.*

Sections of immature florets showed that the stigma of the male florets is at first two lobed as is the hermaphrodite stigma (Cf. Figs. 3A and B). At a later stage in development, however, the two lobes coalesce to form the mature undivided stigma. The existence of sweeping hairs of a similar type at the ends of both the hermaphrodite stigma and the male stigma would seem to suggest that if the two lobes of the hermaphrodite stigma, for some reason joined together during their development, and in consequence lost their stigmatic papillae, the resulting stigma would resemble the male stigma in appearance. It may be that a change of this nature was responsible for the type of stigma which occurs in the disc florets of two Australian species investigated, belonging to the section Strongylosperma—*Cotula alpina* and *C. reptans.* These have the Eucotula-Strongylosperma type of female floret combined with the *Leptinella* type of male disc floret with a flat-topped stigma, instead of the hermaphrodite floret with bifid stigma which might be expected on analogy with *C. australis,* another member of this section. The species of Strongylosperma are therefore, not uniform, some being close to Eucotula—*C. australis,* and others approaching Leptinella—*C. alpina* and *C. reptans.* This combination of floret types suggests that Strongylosperma is intermediate between Eucotula and Leptinella. (Table I.)

TABLE I.—TYPES OF FLORET OCCURRING IN THE GENUS *COTULA.*

TYPE	DESCRIPTION	OCCURRENCE
Female apetalous	Stipitate. Corolla absent. Ovary winged, notched at the top. Bifid stigma sunk in notch.	Eucotula Strongylosperma
Female, corolla present	Sessile or shortly stipitate. Corolla of two layers, inflated at the base, narrowed at the mouth into small teeth, sometimes tubular and lobed. Ovary hardly winged.	Leptinella
Hermaphrodite	Shortly stipitate. Corolla tubular, broadening to a four-lobed mouth. Stigma bifid, achenes smaller than in female with narrower wings.	Eucotula Strongylosperma
Male	Sessile. Corolla tubular, broadening to a four-lobed mouth. Stigma discoid and undivided without stigmatic papillae. Achenes minute and abortive.	Leptinella Strongylosperma (*Cotula alpina*) (*Cotula reptans*)

VARIATIONS IN THE PROPORTION OF THE SEXES IN THE CAPITULUM

As dioecy in *Cotula* occurs only in New Zealand, it is possible that some species might still be variable and show a transition from monoecy to dioecy. Already Hooker (1854), Kirk (1899) and Simpson (1952) had noted species that were not constant in this respect. Hooker (1854) in the "*Flora Novae-Zelandiae*" writes of the monoecious *Leptinella minor*, ". . . sometimes I find many flowers of one sex only in each capitulum, whence the plant is occasionally dioecious." Kirk (1899), describing *Cotula pulchella*, which is dioecious, says, "Heads occasionally slightly heterogamous, one or two female florets being found in the outer row of male florets and more rarely a male floret in the centre of the female head." In 1952 Simpson described a new variety of the dioecious *Cotula pyrethrifolia* which he termed var. *robusta*. He notes that, "The heads in both the species and the variety are not uncommonly bisexual in irregular pattern. In some heads the phenomenon appears to be due to some distortion, in others no distortion is apparent."

Some of the other species were investigated to see if they showed similar variation.

(1) MONOECIOUS SPECIES

(A) *Cotula Haastii*

Heads were collected, one from each plant, from a natural population of *Cotula Haastii* at Evans Pass, and the number of female and male florets in these heads was counted. (Table II.) There was no marked difference in the proportion of female and male florets in any of the heads from this locality.

TABLE II.—PERCENTAGES OF ♀ AND ♂ FLORETS IN HEADS FROM A NATURAL POPULATION OF *C. Haastii*. EVANS PASS, 27/12/55.

Total Florets	% ♀	% ♂
145	48.9	51.1
151	45.7	54 3
144	43.0	57.0
88	48.8	51.2
95	35.7	64.3
96	45.8	54.2
149	59.7	40.3
167	54.4	45.6
107	34 5	65 5
169	50.3	49 7
140	60.7	39.3
120	51 6	48.4
125	48 0	52.0
144	59 0	41.0
Mean	49.01	50.99
Standard error	± 2.14	± 2.14
Variance	64.18	64 18

However, one plant of *Cotula Haastii* was found in a different part of Banks Peninsula, at Mt. Evans, which showed a greater proportion of male florets than was usual in the heads from the first population, and moreover this greater proportion was found in every head from this plant. (Table III.) This was an odd plant, for no others that were predominantly male were found in that area.

(B) *Cotula pectinata*

Table IV shows the percentage of male and female florets in heads from a natural population of *C. pectinata*.

TABLE III.—PERCENTAGE OF ♀ AND ♂ FLORETS ON HEADS OF A SINGLE PLANT OF *C. HAASTII*. MT. EVANS, MAY, 1956.

♀ Florets	♂ Florets.	Total Florets	% ♀	% ♂
35	104	139	25.2	74.8
34	96	130	26.1	73.9
23	60	83	27.7	72.3
13	75	88	14.7	85.3
21	67	88	23.8	76.2
42	96	138	30.4	69.6
15	57	72	20.8	79.2
25	74	99	25.2	74.8
20	83	103	19.4	81.6

TABLE IV.—PERCENTAGE OF ♀ AND ♂ FLORETS IN HEADS FROM A NATURAL POPULATION OF *C. PECTINATA*. PORTERS PASS, 9/1/56.

Total Florets.	% ♀	% ♂
62	54.8	45.2
129	41.8	58.2
90	60.0	40.0
98	57.1	42.9
123	57.7	42.3
158	25.3	74.7
137	45.2	54.8
119	36.1	63.9
101	62.3	37.7
61	47.5	52.5
96	40.6	59.4
140	47.8	52.2
106	40.5	59.5
122	62.3	37.7
84	60.7	39.3
169	51.4	48.6
106	53.8	46.2
103	51.4	48 6
115	38 3	61.7
114	47.4	53.7
127	50.4	49.6
97	38 1	61 9
117	48.9	51.1
109	59.5	40.5
126	42.0	58.0
93	35.5	64 5
113	68.1	31.9
116	39 6	60.4
84	59 7	40.3
120	40.8	59.2
Mean	48 82	51.18
Standard error	± 1.80	± 1.80
Variance	102 59	102.59

(C) *Cotula minor*

Cotula minor, which Hooker considered a variable species, was next investigated. Cheeseman (1925) had said, "Female florets in 3–4 series . . . disc florets fewer in number." However, one plant observed, from L. Ohau, had more male florets than female (Table V), though in all other respects it agreed with Cheeseman's description. Single heads were dissected from specimens of *Cotula minor* in the Auckland Institute and Museum herbarium, which had several heads, and two plants were found which were wholly male, and also two plants which were predominantly though not entirely, female.

TABLE V.—PERCENTAGE OF ♀ AND ♂ FLORETS ON HEADS OF A PLANT OF *C. MINOR* (COLLECTED FROM L. OHAU).

♀ Florets.	♂ Florets.	Total Florets.	% ♀	% ♂
7	29	36	19.4	80.6
5	29	34	14.7	85.3
8	29	37	21.6	78.4
5	23	28	17.8	82.2
5	28	33	15.1	84.9
7	24	31	22.6	77.4
4	20	24	16.6	83.4
6	30	36	16.6	83.4

STATISTICAL ANALYSIS OF TABLES II–V

(1) Tables II and IV. (Natural populations of *Cotula Haastii* and *C. pectinata.*)

The average percentage of female florets is very similar in the two populations—49.01% for *C. Haastii* and 48.82% for *C. pectinata.* The variation in the proportion of the sexes is greater in the population of *C. pectinata* but not significantly so. In the heads examined the percentage of female florets ranges from 34·5%—60.7% in *C. Haastii* and from 25·3%–68·1% in *C. pectinata.*

(2) Tables III and V. (Single plants of *C. Haastii* and *C. minor.*)

The data for the percentage of female florets presented in Tables III and V were analysed in an analysis of variance. This showed that the proportion of female florets differed significantly.

In the two plants examined the average percentage of female florets—23·7% for *C. Haastii* and 18.05% for *C. minor*—is a little lower than the percentage of female florets found on any of the heads in the natural populations of *C. Haastii* or *C. pectinata.*

There is less variation within a single plant in the proportion of the sexes than there is between plants in a natural population. From the analysis of variance, the variation within plants is found to be such that it can be predicted that 5% of the heads of a plant would be expected to differ from the average percentage of female florets by 8% or more.

(D) *Cotula Traillii* and *C. potentillina*

Cotula Traillii is a monoecious species which is predominantly male. One plant collected from Stewart Island had very few female florets. For instance, one head examined had 52 male florets but only 8 female florets or 13%. In contrast to this the monoecious species *Cotula potentillina* from the Chatham Islands, which Kirk considered very similar to *C. Traillii,* has a greater proportion of female florets.

2. DIOECIOUS SPECIES

Four examples of dioecious species with occasional monoecious members were found in addition to those referred to by Kirk and Simpson.

(A) *Cotula pyrethrifolia*

A monoecious example of *Cotula pyrethrifolia* was found on Mt. Hutt. The plant did not differ from *C. pyrethrifolia* in other respects. A different monoecious example of *C. pyrethrifolia* was found at Temple Basin by Miss E. E. Balfour. Here the sexes were confined to different heads, for the plant had 1 completely female head and 2 heads that were completely male. This is the only example of this type of monoecious *Cotula* found among the plants observed, or reported in the literature.

(B) *Cotula squalida*

A monoecious plant of *Cotula squalida,* collected by Petrie from Matata, was found in the Dominion Museum herbarium. The heads on this plant were smaller

than is usual in *C. squalida,* but in other respects the plant did not differ from the usual type. A male plant of *C. squalida* was found on the side of the Otira Gorge Road on which there was a head that had one outer female floret. The plant did not differ from the normal *Cotula squalida* except that the florets had brown-tipped corolla-lobes.

(C) An unclassified *Cotula*

In April, 1955, a plant of *Cotula,* which could not be readily assigned to any species, was collected from the side of the Otira Gorge Road. It appeared distinct from plants of *Cotula squalida* growing nearby, for the leaves were stiff instead of flaccid, or a darker, shinier green in colour, and their pinnae were much less subdivided, if at all. The plant collected flowered in December and the flower heads were, on the average, very much smaller than those of a normal *Cotula squalida,* usually having only 20–30 florets in each head. Most of the florets were male, but in heads where the disc florets had not opened, one or two female stigmas could be seen protruding beyond the bracts at the edge of the head. The heads of this plant were therefore monoecious, in contrast to the dioecious plants of *Cotula squalida* which grow in the same locality. The numbers of male and female florets in each head were counted for over 20 heads, and it was found that there were commonly 1–3 female florets in each head, in one instance 4, in another as many as 6, but that occasionally there were no female florets in a head at all. (Table VI.)

TABLE VI.—PERCENTAGE OF FEMALE AND MALE FLORETS ON HEADS OF ONE PLANT OF *COTULA*. OTIRA GORGE ROAD. JANUARY, 1956.

♀ Florets	♂ Florets	Total Florets	% ♀	% ♂
1	28	29	3.4	96.6
2	21	23	8.7	91.3
3	31	34	9.0	91.0
1	27	28	3.6	96.4
1	29	30	3.3	96.7
0	29	29	0.0	100.0
0	28	28	0.0	100.0
3	26	29	10.3	89.7
3	34	37	8.1	91.9
1	34	35	2.8	97.2
1	24	25	2.5	97.5
2	30	32	6.2	93.8
3	37	40	7.5	92.5
6	23	29	20.7	79.3
0	25	25	0.0	100.0
2	27	29	6.9	93.1
1	27	28	3.6	96.4
4	26	30	13 3	86.7
1	24	25	2.5	97.5
1	28	29	3.4	96.6
3	30	33	9.0	91.0
2	25	27	7.4	92.6
1	21	22	4.5	95.5

To sum up, this *Cotula* could be considered a predominantly male plant which differed from *Cotula squalida* in the following characters:—

(a) It was monoecious, not dioecious like *Cotula squalida.*

(b) It had smaller heads than *Cotula squalida.* The average number of florets in a head was 29 in this plant, whereas in *Cotula squalida* there are generally more than 35 florets in one head.

(c) The stems in this plant burrowed under the ground, but the stems of *Cotula squalida* crept along the surface of the ground.

(d) The leaves of this plant were stiffer, shinier and not so hairy as those of *Cotula squalida.* Their pinnae were not so much subdivided as in the leaves of *Cotula squalida.*

(e) The female florets differed in the two plants. The corolla in *Cotula squalida* is short and very inflated, with only a trace of teeth at the mouth. In the plant from Otira Gorge the female florets had longer corollas which were definitely toothed at the mouth. The stigma was not so much divided in the plant from Otira Gorge as it is in *Cotula squalida.*

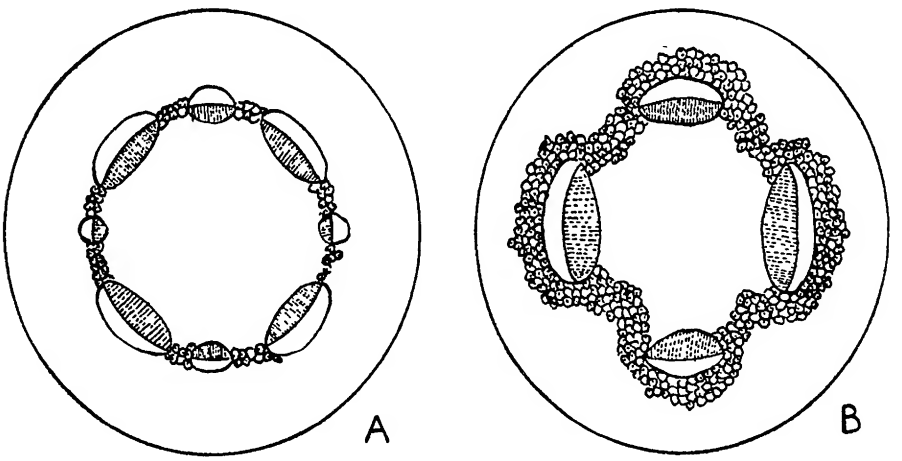
(f) In the male floret of the *Cotula* from Otira Gorge, the corolla widens much more at the mouth than in *C. squalida,* and the corolla lobes are longer.

(g) The achenes of *Cotula squalida* are rounded at the back and almost triangular, whereas in the other plant the achenes are not rounded at the back but flattened, and so disc shaped.

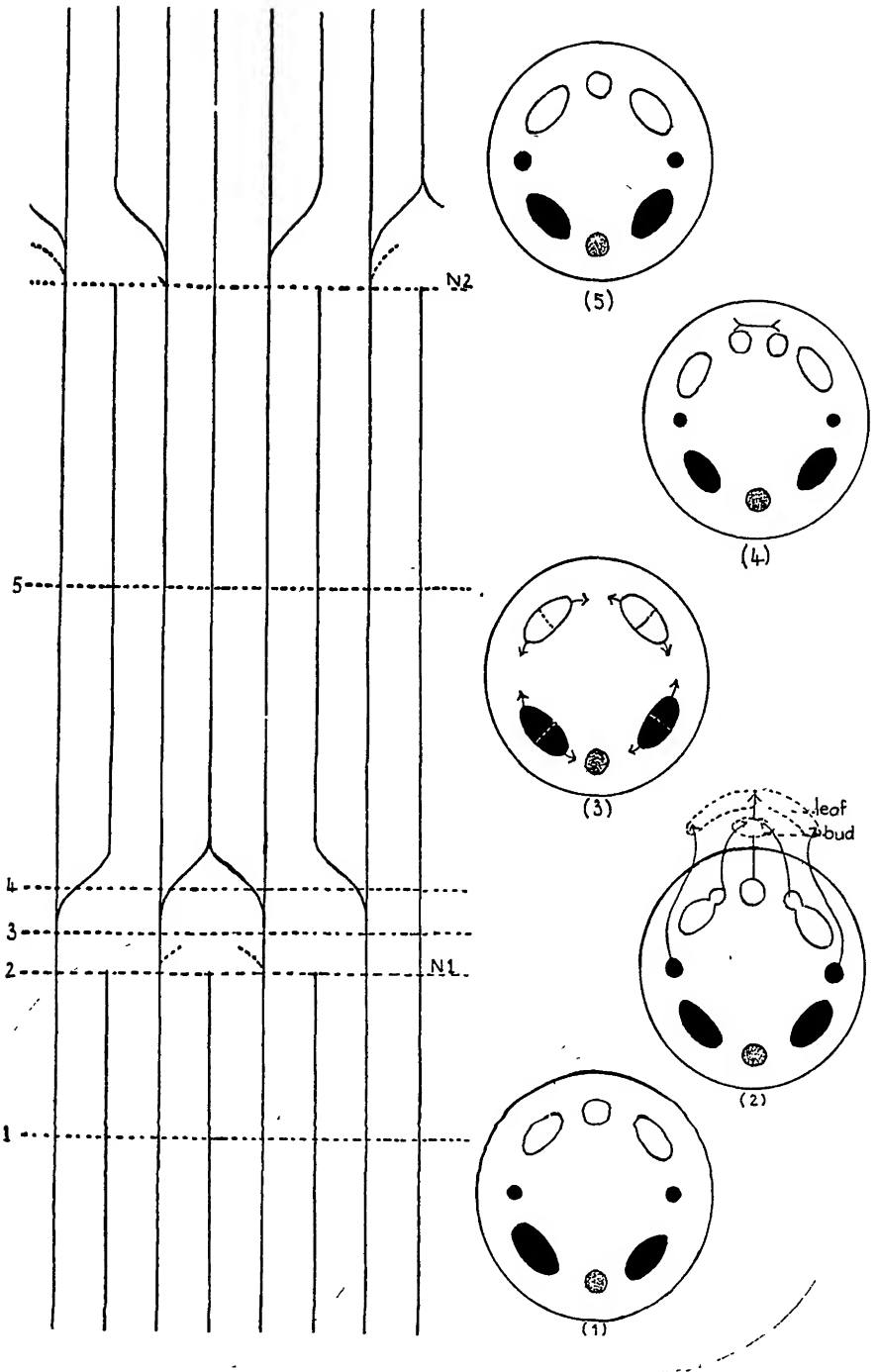
Two Groups in the Section Leptinella in New Zealand

Hooker (1867) and subsequently Kirk (1899) and Cheeseman (1925) subdivided the New Zealand species belonging to the section Leptinella into two groups—one with bisexual heads, the other with unisexual heads. However, it has already been shown that in three species, *Cotula minor, C. pyrethrifolia* and *C. squalida,* both monoecious and dioecious examples occur, while in two monoecious species, *Cotula Traillii* and *C. potentillina,* the ratio of the sexes is unbalanced and the species show an opposite bias, the one towards the male sex—the other towards the female. Dioecy and monoecy are therefore not invariably diagnostic characters. From a study of stem anatomy, however, it was found that the New Zealand members of the Leptinella section could all be definitely assigned to one or other of two groups.

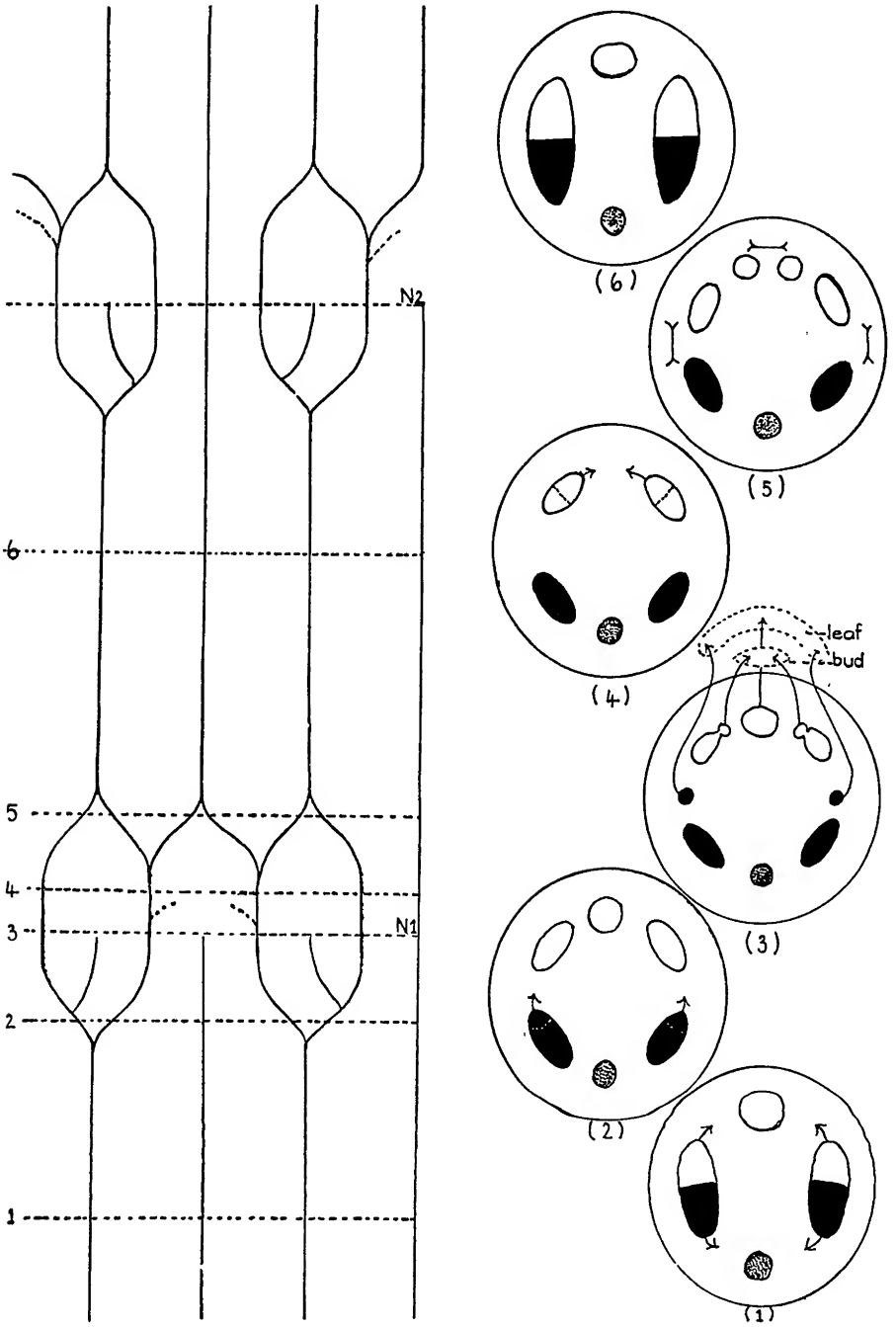
In the first group stem sections showed a ring of 8 vascular bundles (Fig. 4A). Four bundles of this ring were equal in size, and alternating with these were two pairs of opposite bundles, one pair being slightly smaller than the main four, and the other pair being very much smaller. Between all these bundles were narrow bands of fibres running from the xylem group of one bundle to the xylem group in the next. Species with this type of stem were: *Cotula Haastii, C. pyrethrifolia, C. atrata, C. plumosa, C. lanata, C. Maniototo, C. filiformis, C. pectinata, C. Willcoxii,*



TEXT-FIG. 2.—FIG. 4—A. Diagram of T.S. stem of *C. Haastii* (Group I). B. Diagram of T.S. stem of *C. squalida* (Group II).



TEXT-FIG. 3.—FIG. 5—Diagram of vascular system of stem of *C. Haastii* and cross sections through a node.



TEXT-FIG. 4.—FIG. 6—Diagram of vascular system of stem of *C. squalida* and cross sections through a node.

C. Goyeni, C. Featherstonii, C. Renwickii, and *C. linearifolia.* The most noticeable feature of the stem sections of species belonging to the second group was a continuous ring of pericycle fibres. This ring enclosed four vascular bundles (Fig. 4B)—an opposite pair of large bundles and an opposite pair of smaller ones. Species which had stems of this type were *Cotula squalida, C. dioica, C. perpusilla, C. pulchella, C. minor, C. Traillii* and *C. potentillina.* The plant from Otira Gorge also belonged to this group.

Since there was a difference in the number of vascular bundles in the two types of stem—the first group having 8 bundles, the second group having only 4—it was thought that the number of bundles constituting a leaf trace might differ in the two groups. A comparison was therefore made of serial sections through a node of one species from each group—i.e., *Cotula Haastii* from Group I and *C. squalida* from Group II.

The arrangement of the eight bundles in the internode of *Cotula Haastii* (Group I) is shown in Fig. 5 (1). At the node (Fig. 5 (2)), one of the medium sized bundles passes out as the median leaf trace and the two little bundles form the lateral leaf traces. Of the five remaining bundles (Fig. 5 (3)) the four large ones divide in two (Fig. 5 (4)) and two of the resulting nine bundles join together over the gap left by the median leaf trace. Thus the eight bundles of the internode are again reconstituted (Fig. 5 (5)). The bundle which remained unchanged throughout this node (dotted in Fig. 5) passes out to the leaf at the next node with the two little bundles again forming the lateral leaf traces (Fig. 5).

For the greater part of the internode of *Cotula squalida* (Group II) there are only four bundles present (Fig. 6 (1)), but before the node is reached the two large bundles divide in two (Fig. 6 (2)) and from two of these a further pair of very small bundles arises (Fig. 6 (3)). The number and arrangement of the bundles at the node is therefore the same as in *Cotula Haastii* (Cf. Figs. 6 (3) and 5 (2)), and again three bundles supply a leaf—one medium sized bundle and the pair of small bundles. Once more five bundles remain (Cf. Figs. 6 (4) and 5 (3)) but in *Cotula squalida* only two of these divide further so that there are only seven bundles present (Fig. 6 (5)) instead of nine bundles as in *Cotula Haastii* at this stage (Fig. 5 (4)). In *Cotula squalida* six of these bundles join together to form three bundles and so give the internode number of four (Fig. 6 (6)). As in *Cotula Haastii,* the bundle opposite the one which passed out to the midrib of the leaf, remains unchanged throughout this node and passes out as the median bundle of the trace above (Fig. 6).

The difference in number of bundles, therefore, between stems of the two groups is more apparent than real, and the number of bundles constituting a leaf trace is the same in both groups. The fundamental difference, however, lies in the degree of cohesion between the bundles. In *Cotula Haastii* the eight bundles are discrete throughout the internode, but in *Cotula squalida* each of the two large bundles in the internode is formed by the fusion of two bundles which only separate just below the node. The formation of the two little bundles which become the lateral leaf traces is delayed in *Cotula squalida* until the node at which they pass out is reached, whereas in *Cotula Haastii* they are formed at the node below, and run the whole length of an internode before they pass out (Cf. Figs. 5 and 6). The two types of stem also differ in the distribution of the fibres. In the stems of species belonging to Group I, they are in small bands between the bundles, whereas in Group II there is a continuous ring of pericycle fibres.

This grouping of the endemic New Zealand *Cotulas* on the basis of their stem anatomy corresponds to some extent with their grouping according to the distribution of the sexes, although there are exceptions. The majority of the monoecious species belong to Group I, that is *Cotula atrata, C. lanata, C. Maniototo, C. filiformis, C. Haastii, C. pectinata, C. Goyeni, C. Willcoxii, C. Renwickii* and *C. plumosa.* The two exceptions in this group are *Cotula pyrethrifolia* and *C. linearifolia.* These

TABLE VII.—THE TWO GROUPS IN THE NEW ZEALAND LEPTINELLAS

GROUP I

Species	Stem type	Flower colour (where known)	Breeding system	Habit (where known)	Range
Cotula atrata	8 vascular bundles – fibres between bundles	Red purple (C. atrata var. Dendy: yellow & purple	monoecious	patch-forming	South Island shingle slides
C. lanata	8 vascular bundles – fibres between bundles	yellow	monoecious		Auckland and Campbell Island
C. plumosa	8 vascular bundles – fibres between bundles	yellow	monoecious		Auckland and Campbell Island
C. maniototo	8 vascular bundles – fibres between bundles	cream	monoecious	patch-forming	South Island
C. filiformis	8 vascular bundles – fibres between bundles		monoecious	patch-forming	South Is, Canterbury Plains
C. Haastii	8 vascular bundles – fibres between bundles	cream	monoecious	patch-forming	South Island, Banks Peninsula
C. pectinata	8 vascular bundles – fibres between bundles	cream with one broad stripe on carol la, 2 purple stripes on achene	monoecious	patch-forming	South Island
C. Gayeri	8 vascular bundles – fibres between bundles		monoecious		South Island, Central Otago
C. Willcoxii	8 vascular bundles – fibres between bundles	cream disc florets purplish inside	monoecious		South Island, Central Otago
C. Renwickii	8 vascular bundles – fibres between bundles		monoecious		Chatham Islands
C. Featherstonii	8 vascular bundles – fibres between bundles		monoecious		Chatham Islands
C. pyrethrifolia	8 vascular bundles – fibres between bundles	cream	dioecious – has monoecious variants	patch-forming	South Island, river beds and shingle above 2,500 feet
C. linearifolia	8 vascular bundles – fibres between bundles		dioecious		South Island

TABLE VII.—THE TWO GROUPS IN THE NEW ZEALAND LEPTINELLAS

GROUP II

Species	Stem type	Flower colour (where known)	Breeding system	Habit (where known)	Range
C. dioica	4 vascular bundles – complete ring of pericycle fibres	yellow-green	dioecious	turf-forming	North and South Islands
C. squalida	4 vascular bundles – complete ring of pericycle fibres	yellow-green	dioecious	turf-forming	North and South Islands
C. perpusilla	4 vascular bundles – complete ring of pericycle fibres	yellow-green	dioecious	turf-forming	North and South Islands
C. potentillina	4 vascular bundles – complete ring of pericycle fibres		monoecious, predominantly female		Chatham Islands
C. Traillii	4 vascular bundles – complete ring of pericycle fibres	yellow-green	monoecious, predominantly male	turf-forming	Stewart Is & Bluff (Sth Is)
C. minor	4 vascular bundles – complete ring of pericycle fibres	yellow-green	monoecious, has dioecious variants	turf-forming	North and South Islands
Cotula (Otira Gorge Road)	4 vascular bundles – complete ring of pericycle fibres	yellow-green	monoecious, predominantly male	turf-forming	South Island Otira Gorge Rd

are dioecious but have the Group I stem type. The other dioecious species—*Cotula dioica, C. squalida, C. perpusilla* and *C. pulchella*—have the Group II stem type and the monoecious exceptions in this group are *Cotula minor, C. Traillii, C. potentillina* and the *Cotula* from Otira Gorge. However, all these exceptions are species which either show variation in the distribution of the sexes—both monoecious and dioecious forms being found—or else have an unequal ratio of the sexes in the heads. So that the correlation between stem type and distribution of the sexes holds for all species in which there is an even ratio of the sexes.

An attempt was then made to find further correlations to support this division of the species into two groups. Flower colour proved to be one. In the first group the florets are variously coloured. In *Cotula atrata* they are such a dark red-purple that the whole head appears black. Its variety *Dendyi,* in which the florets are a bright sulphur yellow, interbreeds with *C. atrata* to give florets that are intermediate in colour, being various shades of brown, Cockayne (1914) and Cockayne and Allan (1926). *Cotula pectinata* has creamy-white florets with one purple stripe running from the centre of one corolla lobe down to the nectary, where it tapers to a point, and there is a purple stripe on either side of the ovary in both male and female florets. The cream-coloured tubular male florets of *Cotula Willcoxii* broaden to a wide throat which is light brownish-purple inside. *Cotula plumosa* and *C. lanata* have yellow florets and *C. pyrethrifolia* and *C. Haastii* creamy-white. The florets of species in Group II are, however, invariably yellow-green, a colour which does not occur in species of the first group.

It is also possible that there is an ecological difference between species of the two groups, both in their manner of growth and perhaps in the type of soil in which they are found. For of the *Cotulas* which were observed in the field, those belonging to Group I—*Cotula Haastii, C atrata, C pectinata, C. Maniototo* and *C. pyrethrifolia*—grew in small tufts and rosettes with bare patches of ground between them; whereas *Cotula squalida, C. dioica, C. Traillii* and *C. minor* of Group II had long runners which scrambled over the surface of the ground making a thick mat Cockayne (1927), giving the life-form of *Cotulas* found in Canterbury, used two different terms to describe them, " patch-forming herb " and " turf-forming herb ". He described *Cotula Maniototo* and *C. filiformis* (Group I) as " patch-forming herbs " and *Cotula perpusilla* and *C. squalida* (Group II) as " turf-forming herbs ". Species of Group I which were observed in the field grew on high exposed faces, or dry river beds above 2,500 feet. Altitude, however, by itself, appears to have no bearing on this grouping, for *C. squalida* (Group II) is found at 3,000 feet at Arthurs Pass where *C. pyrethrifolia* (Group I) is found not far away. But soil conditions that are often associated with altitude are avoided by *Cotula squalida* which is not found in newly eroded ground but only in proximity to other herbs whose decay has provided some humus. On the other hand *C. atrata* (Group I) is a shingle slide plant and *C. pectinata* (Group I) is found on eroded slopes, solitary, in the bare soil.

There may also be a difference in distribution between the species belonging to the two groups. The only species of *Cotula* which are reported by Cheeseman as being widespread in the North and South Islands belong to Group II—i.e., *Cotula dioica, C. squalida, C. perpusilla* and *C. minor,* whereas the species of Group I, in contrast, are confined to the South Island and its outlying extensions, the Chathams and the Auckland and Campbell Islands.

Table VII gives a list of the species in the two groups and of the characters which it is thought may distinguish these two groups.

Part II.—Floral Biology

Abstract

THE type of fertilization in some New Zealand *Cotulas* was investigated and the gynomonoecious and monoecious species examined were found to be self-fertile. No examples of apomixis were found in these species or in dioecious species examined.

In the monoecious species the first female florets were found to open 3–7 days before the first male florets opened, so that only the stigmas of the innermost row of female florets were receptive when the first male florets opened.

The percentage of fruit set on isolated plants of *Cotula Haastii* and *C. pectinata* and on plants from natural populations of these species was estimated.

It is considered that *Cotula* is insect pollinated and a list of some insect visitors to *Cotula coronopifolia, C. Haastii, C. pectinata, C. squalida* and *C. dioica* is given.

INTRODUCTION

BETWEEN the two extremes of the self-fertile hermaphrodite, which may be completely inbreeding, and the dioecious type, in which outbreeding is obligatory, lie other intermediate systems which allow, to varying degrees, both inbreeding and outbreeding. In *Cotula* the two extreme systems are to be found—viz., the South African species with all florets hermaphrodite, and the dioecious New Zealand species. But two intermediate systems—gynomonoecious species, in which the outer florets are female and the inner hermaphrodite, and monoecious species, in which the outer florets are female and the inner male—are also to be found in *Cotula,* both with examples in New Zealand.

TYPE OF FERTILIZATION

In New Zealand both the gynomonoecious species, and the monoecious species, as far as observed, are self-fertile. This was found by self-pollinating isolated plants of *Cotula coronopifolia* and *C. australis* which are gynomonoecious, and *Cotula Haastii, C. pectinata, C. Maniototo* and *C. atrata* which are monoecious. Seed was set on both the female and hermaphrodite florets in the gynomonoecious species, and on the female florets in the monoecious species. Whenever isolated plants set fruit, however, the possibility that the plants may be apomictic must be considered. The percentage of fruit set on heads of isolated plants of *Cotula Haastii, C. pectinata, C. minor* and *C. Traillii* was always very low in comparison with plants in natural populations, whereas if they had been apomictic, a similar percentage would have been expected. In *Cotula coronopifolia* the central hermaphrodite florets were removed and the heads covered with nylon bags before the female florets had matured. No fruit was set on these heads. It is therefore concluded that this species also is not apomictic Two dioecious species *Cotula squalida* and *C. dioica* were investigated for apomixis. One female plant of *Cotula dioica* from Bexley Road, South Brighton, was grown in a garden in Christchurch in the open and flowered freely. As none of the heads set fruit it is concluded that this plant was not apomictic. Heads of a female plant of *Cotula squalida,* collected from Arthur's Pass and grown in the same garden, were covered with nylon bags and set no fruit. This plant, then, was not apomictic either.

Both gynomonoecious and monoecious types, however, have a flexible breeding system, for all the florets may be cross-fertilized. There is, in fact, a certain restriction of self-fertilization since the female florets, situated as they are on the outside of the head, are open for some days before the central florets in the same head are open and in monoecious species it was observed that only the stigmas of the innermost row of female florets were still receptive when the first central male florets opened.

Interval Between Male and Female Anthesis

The difference in time between the opening of the first female florets and the opening of the first male florets was observed in three plants of *Cotula Haastii* all collected from Evans Pass. One plant was grown in the glasshouse at Lincoln, one in a garden at Christchurch in the sun, and one in the same garden in the shade. In the plant growing in the glasshouse, the timing difference in the 1954-55 season ranged from 5–7 days, the average being six days. In the 1956–57 flowering season the timing difference was 7 days in August, but later in the season when temperatures were higher, the difference was shorter, being 5 days. The effect of temperature in hastening anthesis could also be observed in the plants growing at Christchurch. In the 1955-56 flowering season the timing difference in the plant growing in the shade ranged from 3–7 days, the average being 5·3 days. In the plant growing in the sun, however, the difference ranged from 3–5 days, the average being 4·3 days.

Comparison of Fruit Set on Isolated Plants and on Plants in Natural Populations

In an attempt to discover whether there was any significant difference in the amount of fruit set on an isolated plant in the glasshouse and a similar plant forming part of a natural population, the amount of fruit set on the heads of a single isolated plant of *Cotula Haastii,* collected from Evans Pass and grown in the glasshouse at Lincoln, was compared with the amount of fruit set on heads of 16 plants growing in the natural population at Evans Pass. (Table VIII.)

Table VIII.—FRUIT SET ON HEADS FROM (A) AN ISOLATED PLANT OF *COTULA HAASTII,* AND (B) A NATURAL POPULATION OF *COTULA HAASTII.*

(A) Isolated Plant			(B) Natural Population		
Total Florets.	Fruit Set	% Fruit	Total Florets	Fruit Set	% Fruit
104	2	1.9	65	13	20 0
82	3	3.6	60	14	21.6
86	4	4 6	74	4	5 4
85	2	2.3	71	16	22.5
95	0	0 0	69	43	62 3
81	1	1 2	62	7	11.3
76	0	0 0	43	5	11 6
77	1	1 3	34	23	67.6
103	4	3.8	44	32	72.7
76	3	3 9	89	22	24.7
106	10	9.4	30	16	53 3
85	0	0.0	91	61	67 0
127	5	3.9	85	64	75 3
77	2	2 6	62	49	79 0
56	0	0 0	60	43	71.6
			85	63	75 3

The amount of fruit set on heads of a single isolated plant of *Cotula pectinata,* collected from Porters Pass and grown in the glasshouse, was compared with the amount of fruit set on heads collected from plants in a natural population of this species at Porters Pass. (Table IX.)

In most cases the percentage of fruit set in the field is far higher than that set in the glasshouse, for in the field there is every opportunity for both cross-fertilization and self-fertilization by wind or by insects, whereas in the case of the isolated plant in the glasshouse, self-fertilization, in the absence of wind or insects, must be very limited even without the additional restriction caused by the difference in time of opening of the female and male florets.

TABLE IX.—FRUIT SET ON HEADS FROM (A) AN ISOLATED PLANT OF *COTULA PECTINATA*, AND (B) A NATURAL POPULATION OF *COTULA HAASTII*.

(A) ISOLATED PLANT			(B) NATURAL POPULATION		
Total Florets	Fruit Set	% Fruit	Total Florets	Fruit Set	% Fruit
75	6	8.0	34	0	0.0
38	0	0.0	54	7	12.9
36	0	0.0	54	8	14.8
51	3	5.9	56	32	57.1
44	0	0.0	52	0	0.0
37	0	0.0	40	22	55 0
51	0	0.0	62	33	53.2
27	1	3.7	43	1	2.3
47	0	0.0	63	23	36 5
53	0	0.0	29	1	8.4
			39	0	0.0
			67	39	58.2
			43	3	7.0
			76	34	44.7
			51	21	41.1
			87	39	44.8
			57	5	9 6
			53	27	50 9
			44	31	70.4
			54	45	83.3
			33	16	48.5
			38	28	73.7
			33	17	51.5
			29	18	62 0
			29	15	51.7
			34	20	58 8
			64	24	66 6
			37	18	48 6

INSECTS AND THE FERTILIZATION OF *Cotula*

The dioecious species of *Cotula* must depend entirely, and the monoecious species partly, on some external agency for fertilization, and Thomson (1880) thought that *Cotula* was mainly wind-pollinated. "The genus *Cotula* I have hardly looked into. *C. coronopifolia* has very conspicuous yellow flower heads which are destitute of fragrance and produce little or no honey. The minuter flowered forms as *C. dioica, C. minor,* etc., do not seem to possess any attractions for insects. The absolutely unisexual species are probably anemophilous." However, as a number of insects were seen on the flower heads of *Cotula dioica* and *C. squalida* (both dioecious species) and others were seen to visit *C. coronopifolia, C. Haastii* and *C. pectinata* it is considered that insects as well as wind play a part in the fertilization of *Cotula.*

Cotula, indeed, possesses several characters which are thought to be attractive to insects In both male and female florets there is a nectary surrounding the style at the base of the corolla tube; and although the flower heads have no scent, the foliage has a strong odour and there are glandular hairs on both florets and leaves. In addition, the pollen grains have a particularly spiny coat so that they cling to one another in clumps. This sticky type of pollen is generally associated with insect-pollinated rather than with wind-pollinated flowers.

The following is a list of insects seen to visit some species of *Cotula.* The list shows that there was quite a variety of insect visitors, both large and small.

List of Insect Visitors

(A) *Cotula coronopifolia*

Heine (1938) reports immature insects belonging to the family Pentantomidae (Hemiptera).

Blowflies were seen visiting plants in the glasshouse at Lincoln.

(b) *Cotula Haastii*

In December, 1955, red grubs of a fly, which could not be identified at that stage, were found inside mature heads of *Cotula Haastii* growing at Evans Pass. Even if the grubs eat some of the seeds, the loss of seed may be offset by the insect fertilizing the florets when it lays its eggs. Heads which had these grubs always had set plenty of seed.

(C) *Cotula pectinata*

In January, 1956, the same red grub was found in heads of *Cotula pectinata* at Porters Pass.

A blowfly and green aphids were seen sucking the nectar from flowers in the glasshouse at Lincoln.

(D) *Cotula squalida*

In January, 1955, a black puparium of a fly was found in many heads of *Cotula squalida* at Arthur's Pass. The fly, however, could not be identified from that stage. The heads of *Cotula squalida* make an excellent shelter for young insects, since when fruit is set the involucral bracts grow up, and curving over, completely cover the mature achenes. Many of the achenes had not developed in the heads which had these puparia.

In December, 1955, the following insects were caught when visiting plants at Arthur's Pass:—

Coleoptera
Pyronota festiva
Selenopalpus cyaneus
Flea beetle

Hymenoptera
Proctotrypes sp.

Hemiptera
Immature Hemipteran

Thysanoptera
Thrips (3 different kinds)
Fungus gnats—Mycetophilids

(E) *Cotula dioica*

A tortricid moth, which was continually flitting round the leaves of plants of this species, was caught in the glasshouse at Lincoln. A Lepidopterous larva, Tortricidae (adult identity unknown) was also found on the flower head of a plant growing in a Christchurch garden.

In the same garden, the following insects were seen to visit both a male and a female plant:—

Coleoptera
Helodidae (Dascillidae)
Two species of the genus *Cyphon*

Hymenoptera
Formicidae
Monomorium nitidum Smith.

Hemiptera
Jassidae
Erythroneura ansonae Myers.

Aphididae
Cavariella aegopodii Scop.

DIPTERA

Cecidomyiidae
Cecidomyia sp.

Ephydridae
Hydrellia velutifrons Tonn.

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ELIZABETH EDGAR, B.A., M.Sc.,
Botany Department,
University of Canterbury,
Christchurch.